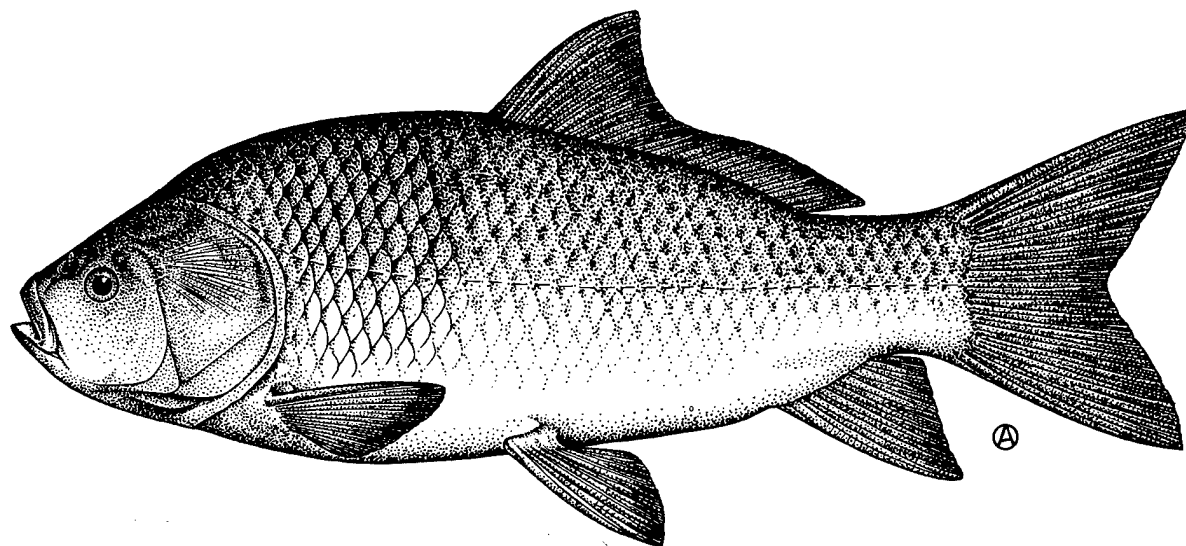
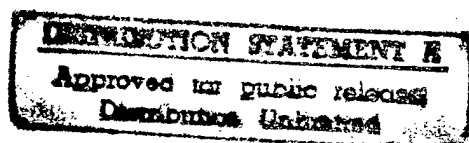


HABITAT SUITABILITY INDEX MODELS: BIGMOUTH BUFFALO



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Fish and Wildlife Service

U.S. Department of the Interior

This model is designed to be used by the Division of Ecological Services
in conjunction with the Habitat Evaluation Procedures.

FWS/OBS-82/10.34
September 1983

HABITAT SUITABILITY INDEX MODELS: BIGMOUTH BUFFALO

by

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PREFACE

The habitat use information and Habitat Suitability Index (HSI) models presented in this document are an aid for impact assessment and habitat management activities. Literature concerning a species' habitat requirements and preferences is reviewed and then synthesized into subjective HSI models, which are scaled to produce an index between 0 (unsuitable habitat) and 1 (optimal habitat). Assumptions used to transform habitat use information into these mathematical models are noted, and guidelines for model application are described. Any models found in the literature which may also be used to calculate an HSI are cited, and simplified HSI models, based on what the author believes to be the most important habitat characteristics for this species, are presented. Preference curves for use with the Instream Flow Incremental Methodology (IFIM) are excluded from this publication. A summary document describing curves for use with IFIM for this species and preceding species publications in this series (82/10) is planned for early 1984.

Use of the models presented in this publication for impact assessment requires the setting of clear study objectives and may require modification of the models to meet those objectives. Methods for reducing model complexity and recommended measurement techniques for model variables are presented in Terrell et al. (1982).¹ A discussion of HSI model building techniques is presented in U.S. Fish and Wildlife Service (1981).²

The HSI models presented herein are complex hypotheses of species-habitat relationships, not statements of proven cause and effect relationships. The models have not been tested against field data. For this reason, the U.S. Fish and Wildlife Service encourages model users to convey comments and suggestions that may help us increase the utility and effectiveness of this habitat-based approach to fish and wildlife planning. Please send comments to:

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¹Terrell, J. W., T. E. McMahon, P. D. Inskip, R. F. Raleigh, and K. L. Williamson. 1982. Habitat suitability index models: Appendix A. Guidelines for riverine and lacustrine applications of fish HSI models with the Habitat Evaluation Procedures. U.S. Dept. Int., Fish Wildl. Serv. FWS/OBS-82/10.A. 54 pp.

²U.S. Fish and Wildlife Service. 1981. Standards for the development of habitat suitability index models. 103 ESM. U.S. Dept. Int., Fish Wildl. Serv., Div. Ecol. Serv. n.p.

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BIGMOUTH BUFFALO (Ictiobus cyprinellus)

HABITAT USE INFORMATION

General

The bigmouth buffalo (Ictiobus cyprinellus) occurs from the Lake Erie drainage south through the Ohio and Mississippi River drainages to the Tennessee River in northern Alabama; west to Arkansas; south to near the Gulf of Mexico in Louisiana; northwest through eastern Texas and Oklahoma; north through Iowa, South Dakota, and Minnesota; and in the Milk River into Manitoba and Saskatchewan. The species has been introduced into reservoirs in Arizona, the Los Angeles aqueduct system in southern California (Trautman 1957; Johnson 1963; Scott and Crossman 1973; Hubbs and Lagler 1974; Moyle 1976; Lee et al. 1980), and reservoirs of the Missouri River drainage in North Dakota and Montana (Lee et al. 1980).

Possible hybridization with the smallmouth buffalo (Ictiobus bubalus) has been reported (Giudice 1964; Johnson and Minckley 1969, 1972). Crosses of bigmouth and black buffalo (Ictiobus niger) exhibit hybrid vigor (Guidice 1964).

Age, Growth, and Food

Sexual maturity in the bigmouth buffalo depends on the size of the fish. Females mature at a length > 475 mm (Johnson 1963). Males begin to mature at 305-328 mm, and most are mature at about 356-379 mm. These sizes correspond to age I for males and II for females in Arkansas (Swingle 1957; Walburg and Nelson 1966). In Lewis and Clark Reservoir, South Dakota, where growth is slower, some males mature at age VII, and most are mature at age VIII (Walburg and Nelson 1966). Some females mature at age VIII, and most are mature at age IX.

An age of XX has been reported for the bigmouth buffalo (Johnson 1963; Lee et al. 1980). However, aging techniques for fishes older than about age X are questionable. Maximum length is reported to be 889 mm (Lee et al. 1980), and the largest reported specimen weighed 36 kg (Harlan and Speaker 1969).

Larval bigmouth buffalo eat benthic copepods and cladocerans (McComish 1964; Starostka and Applegate 1970; Tafaelli et al. 1970) and sometimes phytoplankton (Johnson 1963), chironomids (Starostka and Applegate 1970), and "ooze" (Whitaker 1974). Juveniles and adults occupy a food niche overlapping both benthic and limnetic plankton feeders (Johnson 1963) and consume organisms

according to their availability (Moen 1954; McComish 1964; Minckley et al. 1970; Starostka and Applegate 1970; Tafanelli et al. 1970). They also eat cladocera, copepods, algae, Chironomidae, ostracods, and other insect larvae and invertebrates (Johnson 1963; Minckley et al. 1970; Starostka and Applegate 1970; Tafanelli et al. 1970; Stanley and Jones 1976). Food supply is an important limiting factor for growth (Canfield 1922; Walburg and Nelson 1966).

Reproduction

The addition of fresh water triggers spawning, and year class strength is positively related to rising water levels and flooded terrestrial vegetation (Canfield 1922; Moen 1954; Johnson 1963; Gassaway 1970; Beckman and Elrod 1971; Elrod and Hassler 1971; Benson 1973; Willis 1978; Willis and Owen 1978; Benson 1980). Bigmouth buffalo spawn from April to June (Canfield 1922; Swingle 1957; Johnson 1963; Walburg and Nelson 1966; Benson 1973), when the water temperature reaches 14.4° C (Johnson 1963). Spawning is slow until water temperatures reach 15.6-16.7° C and is heaviest at temperatures of 15.6-18.3° C (Canfield 1922; Johnson 1963). This species will spawn at temperatures up to 26.7° C (Swingle 1954). Bigmouth spawn in shallow water over vegetation and scatter their adhesive eggs randomly (Johnson 1963).

Specific Habitat Requirements

Bigmouth buffalo typically inhabit larger rivers, utilizing overflow ponds, lowland lakes and oxbows, and marshes along these rivers (Gerking 1945; Trautman 1957; Johnson 1963; Kozel and Schmulbach 1976). The species also lives in bayous and sloughs (Gerking 1945) of very low gradient (Johnson 1963). Bigmouth buffalo seek out low velocity areas (0-70 cm/sec) (Schmulbach et al. 1975), but can withstand strong current velocities for short periods (Kallemeyn and Novotny 1977). An adult can maintain its position in a stream velocity of 102.5 cm/sec for a short period, but the mean critical velocity (maximum current velocity at which a fish can maintain its position in the water) is 64.9 cm/sec (Zittel 1978).

Bigmouth buffalo are well adapted to reservoirs (Johnson 1963). The species moves into warm, shallow, protected embayments in the upstream portion of reservoirs during summer and into deeper water in fall and winter (Huntington and Hill 1956; Beckman and Elrod 1971; Benson 1980). Degradation of littoral habitat in reservoirs, due to fluctuating water levels and resulting siltation and erosion, will reduce buffalo populations (Benson 1980). The presence of quiet water embayments and abundant vegetation is also critical. Bigmouth buffalo do well in the first several years of impoundment of a reservoir, or when new land is inundated, but the number of adults decreases in later years (Walburg and Nelson 1966; Elrod and Hassler 1971; Benson 1973; Willis and Owen 1978; Benson 1980).

The standing crop of bigmouth buffalo increases as the storage ratio (SR) (ratio of mean reservoir water volume to annual discharge volume) decreases (Jenkins 1976). Growth of bigmouth buffalo is positively correlated with food supply (Walburg and Nelson 1966) and TDS levels (Jenkins 1967, 1976). Adequate TDS levels in lakes and reservoirs (> 200 TDS) should ensure an adequate food supply to support high population levels.

Bigmouth buffalo can tolerate suspended solids and sediment and do well in turbid waters or over mud bottoms (Trautman 1957; Johnson 1963; Muncy et al. 1979). The species will tolerate turbidity levels > 100 ppm (Walburg and Nelson 1966).

A pH range of 6.5-8.5 is considered essential for good production of freshwater fish (Stroud 1967), and a pH range of 5.0-6.5 or 8.5-9.0 can be detrimental to fish populations (Doudoroff and Katz 1950; Committee on Water Quality Criteria 1972). A pH of 6.5-8.5 is assumed to be optimum for bigmouth buffalo.

The specific dissolved oxygen (D.O.) requirements of bigmouth buffalo are not known, but 5.0 mg/l is considered the minimum level for maintaining good freshwater fish populations (U.S. Environmental Protection Agency 1976).

Successful spawning of bigmouth buffalo occurred in ponds in Louisiana where salinity ranged from 1.4-2.0 ppt (Perry 1976). Life stages from fertilized eggs through yearlings tolerated salinities through 9 ppt in laboratory studies, but water with salinity > 12 ppt is not suitable (Hollander 1974; Hollander and Avault 1975).

Adult. Adult bigmouth buffalo have been collected in warm water temperatures ranging from 22.5-38.0° C near a thermal effluent. Temperature preferenda is 31-34° C (Gammon 1973).

Embryo. Optimum temperatures for incubation and hatching are 15-18° C (Canfield 1922), but eggs will develop at temperatures up to 26.7° C (Swingle 1954). Vegetation is required for successful spawning (Benson 1980). Any drop in water level after spawning will reduce reproductive success (Benson 1973). Shallow backwaters and marshes are required in riverine habitats (Kallemeyn and Novotny 1977) and protected embayments are required for nurseries in lacustrine habitats (Benson 1980).

Even though bigmouth buffalo eggs tolerated salinities up to 15 ppt, newly hatched fry tolerated only 9 ppt (Hollander 1974). Thus, it is assumed that 9 ppt would be the upper tolerance limit for the species.

Fry and Juvenile. Specific environmental information for fry and juvenile bigmouth buffalo is unknown.

HABITAT SUITABILITY INDEX (HSI) MODELS

Model Applicability

Geographic area. The model is applicable throughout the native and introduced range of the bigmouth buffalo in North America. The standard of comparison for each suitability index is the optimum value of the variable that occurs anywhere within this region. Therefore, the model may never provide an HSI of 1.0 when applied to waters in the North where temperature-related variables may not reach the optimum values found in the South.

Season. The model provides a rating for a habitat based on its ability to support a reproducing population of bigmouth buffalo through all seasons of the year. The model will provide an HSI of 0 if any reproduction-related variable indicates that the species is not able to reproduce.

Cover types. The model is applicable in riverine and lacustrine habitats as described by Cowardin et al. (1979).

Minimum habitat area. Minimum habitat area is defined as the minimum area of contiguous suitable habitat that is required for a species to live and reproduce. No attempt has been made to establish a minimum habitat size for bigmouth buffalo, although this species prefers larger rivers and reservoirs.

Verification level. The acceptance level of the bigmouth buffalo model is to produce an index between 0 and 1 that the model author believes has a positive relationship to spawning success of adults and carrying capacity for fry, juveniles, and adults. In order to verify that the model output was acceptable, HSI's were calculated from sample data sets. These sample data sets and their relationship to model verification are discussed in greater detail later.

Model Description

The analysis of habitat quality for bigmouth buffalo is based on basic components consisting of food, cover, water quality, and reproduction requirements. Variables that have been shown to affect growth, survival, abundance, or other measures of well-being of bigmouth buffalo are placed in the appropriate component (Figs. 1 and 2).

Model Description - Riverine

Food-cover component. Food and cover have been aggregated into one component because the same variables describe both food and cover suitability. Percent pools and off-channel areas (V_1) is included because this is where the species spends most of its time and requirements for food and cover must be met in these areas. Percent vegetation (V_{13}) is important because success of bigmouth buffalo populations has been correlated with the presence of vegetation, which is necessary for cover for fry and juveniles and for food production.

Water quality component. Temperature (V_4) is the most important water quality variable because it restricts this warmwater species by its effects on growth and survival. Turbidity (V_2), pH (V_3), and dissolved oxygen (V_6) also affect growth and survival of the species. Bigmouth buffalo can tolerate high salinity (V_8). However, salinity is not usually a problem in areas where the species is found and, thus, is an optional variable.

Habitat variables

Life requisites

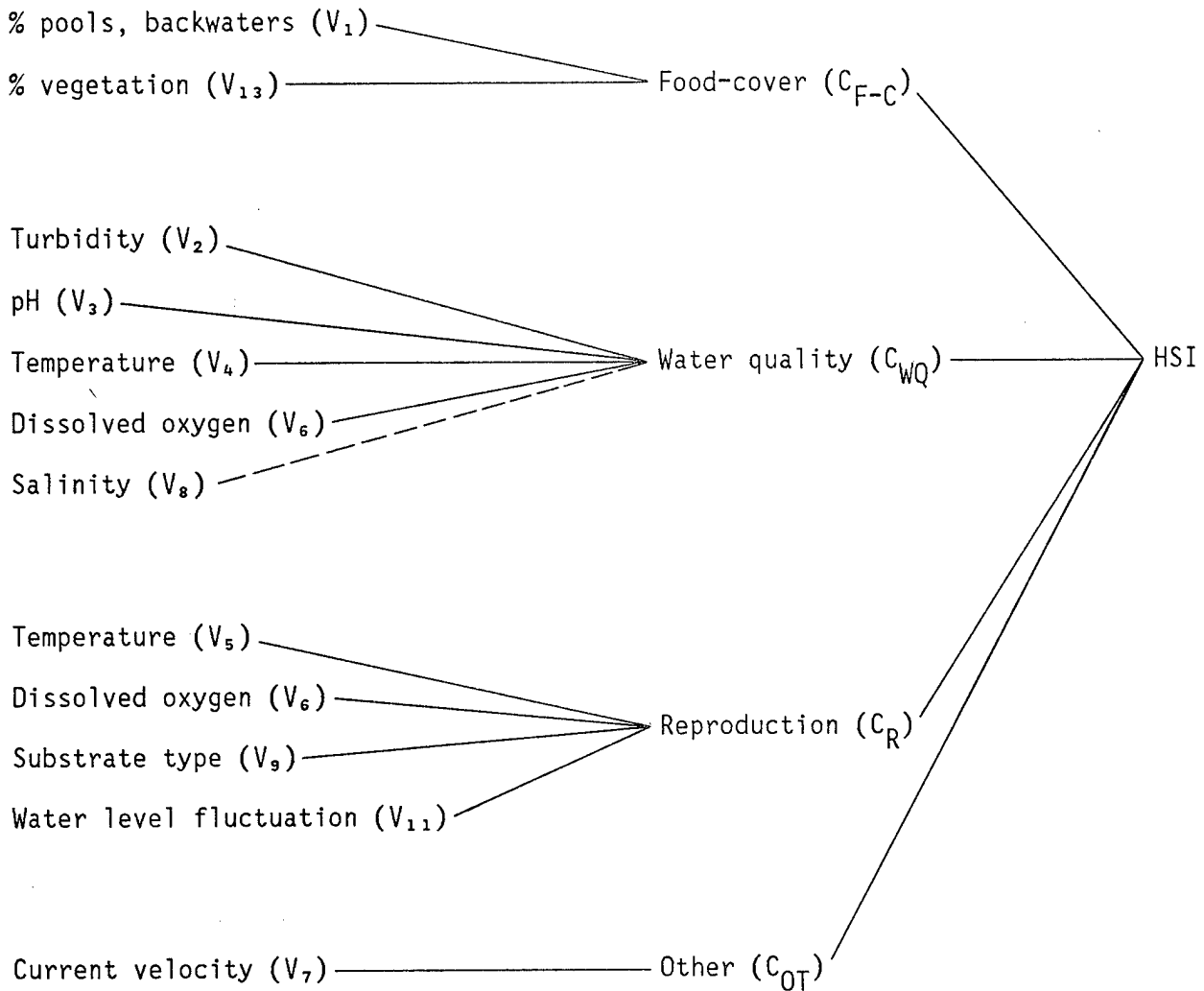


Figure 1. Tree diagram illustrating the relationship of habitat variables and life requisites in the riverine model for the big-mouth buffalo. The dashed line indicates an optional variable in the model.

Habitat variables

Life requisites

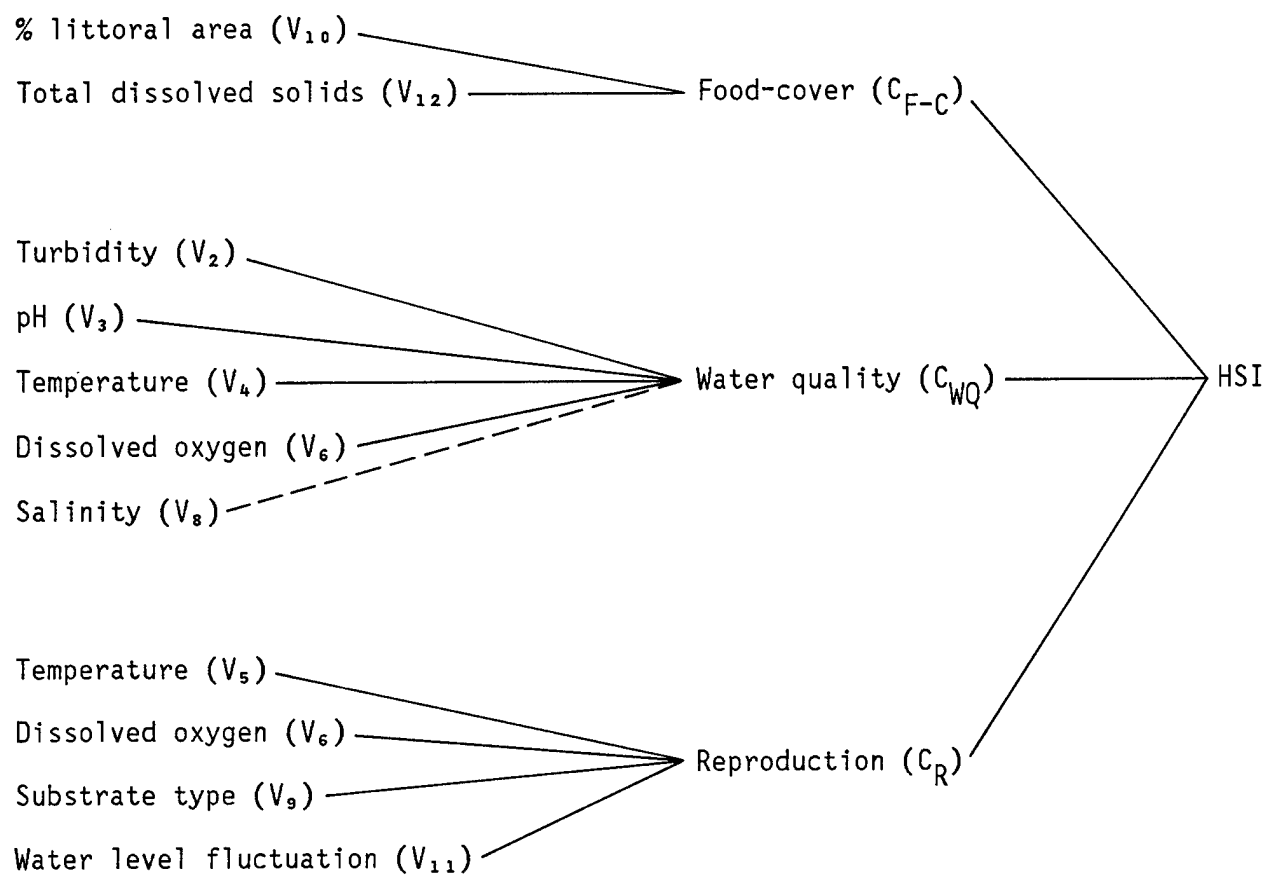


Figure 2. Tree diagram illustrating the relationship of habitat variables and life requisites in the lacustrine model for the bigmouth buffalo. The dashed line indicates an optional variable in the model.

Reproduction component. Temperature during spawning (V_5) and dissolved oxygen (V_6) are included because survival of the embryo depends on these variables. Spawning substrate type (V_9) is a very important variable because reproductive success of bigmouth buffalo is dependent on the presence of vegetation during spawning. Water level fluctuation (V_{11}) is included because flooding with fresh water in the spring "triggers" spawning, rising water levels inundate terrestrial vegetation for spawning substrate, and a drop in water level reduces reproductive success.

Other component. The variable in the other component aids in describing habitat suitability for bigmouth buffalo, but is not specifically related to the life requisite components already presented. Current velocity (V_7) is included because the species actively seeks out areas of low velocity.

Model Description - Lacustrine

Food-cover component. Food and cover are aggregated into one component for the lacustrine model. Percent littoral area (V_{10}) is included because bigmouth buffalo forage in, and inhabit, littoral areas almost exclusively. Total dissolved solids (V_{12}) is important because standing crop of bigmouth buffalo is positively correlated with total dissolved solids, which, in turn, affect the food supply.

Water quality component. The water quality component is the same in both the riverine and lacustrine models. This component is discussed in the description of the riverine model.

Reproduction component. The reproduction component is the same in both the riverine and lacustrine models. This component is discussed in the description of the riverine model.

Suitability Index (SI) Graphs for Model Variables

This section contains suitability index graphs for the 13 variables described above and equations for combining selected variable indices into a species HSI using the component approach. Variables may pertain to either a riverine (R) habitat, a lacustrine (L) habitat, or both.

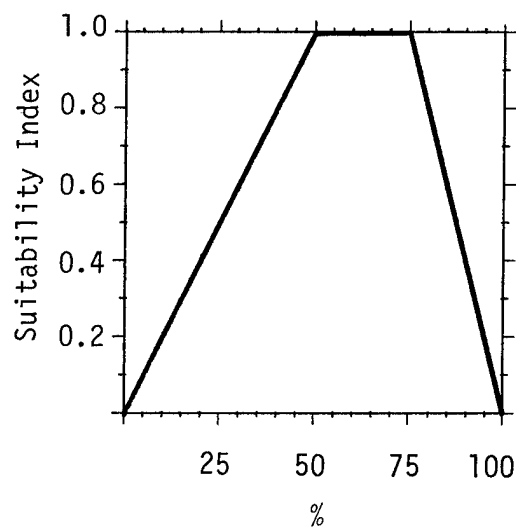
Habitat	Variable
---------	----------

R

V₁

Percent of pools, backwaters, and marsh areas during spring and summer (adult, embryo, juvenile, and fry).

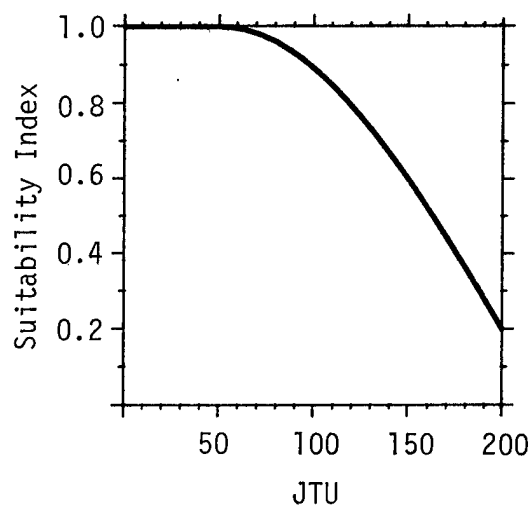
Suitability graph



R,L

V₂

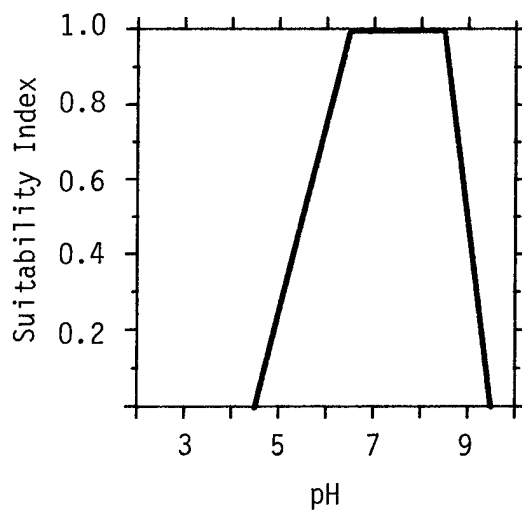
Average maximum monthly turbidity during average summer flow or summer stratification.



R,L

V₃

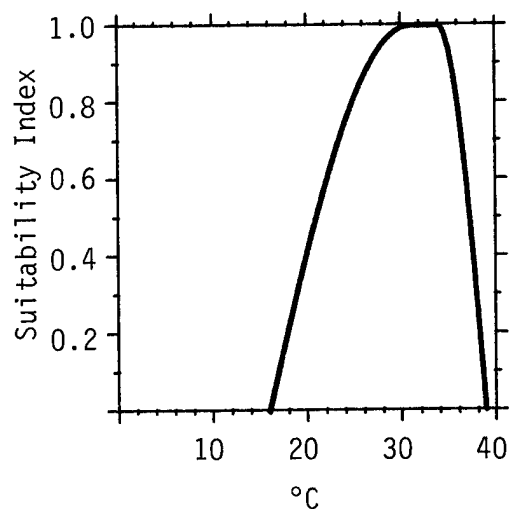
pH levels during the year.



R,L

V₄

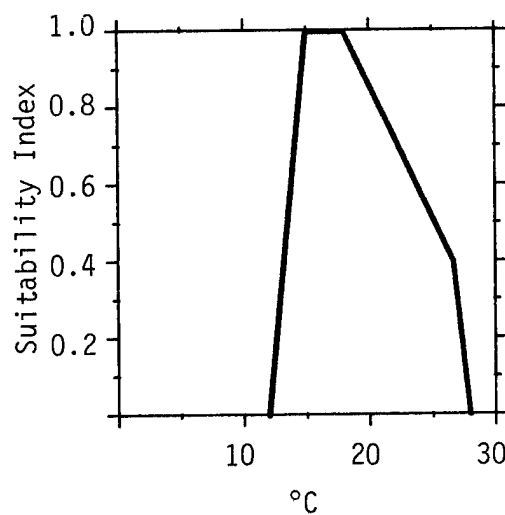
Maximum water temperature where the species occurs in summer (adult).



R,L

V₅

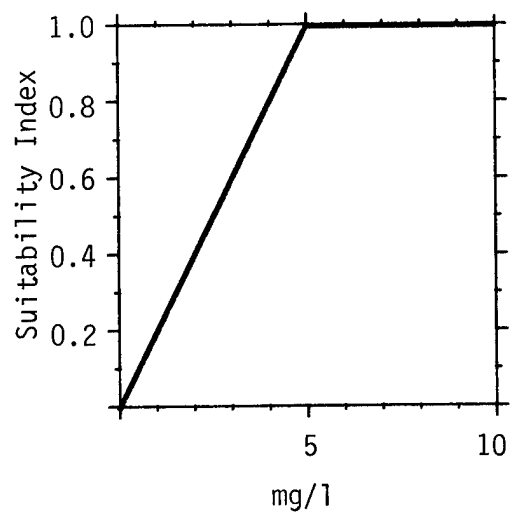
Average maximum water temperatures in nursery habitats during spring and summer (embryo).



R,L

V₆

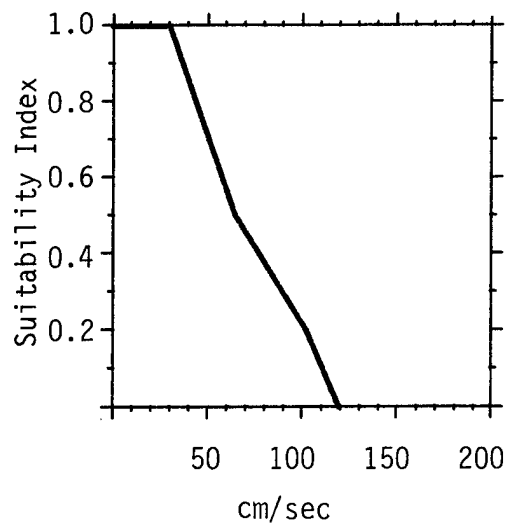
Minimum dissolved oxygen level during spring and summer (embryo-adult).



R

 V_7

Average current velocity.

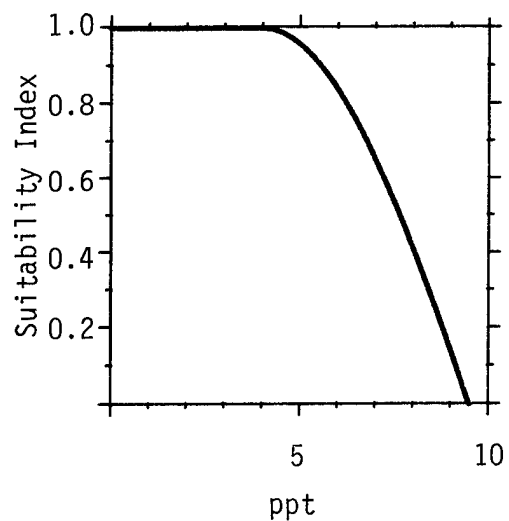


R,L

 V_8

Maximum salinity during spring and summer (embryo-adult).

Note: V_8 can be omitted if salinity is not considered a potential problem in the study area.

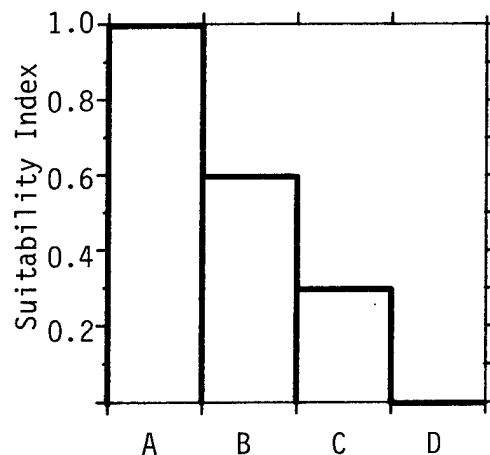


R,L

 V_9

Dominant substrate type in spawning areas (embryo).

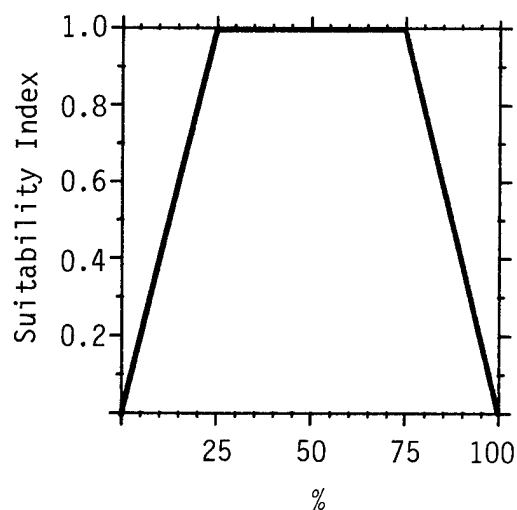
- A. Abundant inundated terrestrial, submergent, or emergent aquatic vegetation.
- B. Some vegetation and submerged objects.
- C. Little vegetation, but some submerged objects.
- D. No vegetation; clear substrate.



L

 V_{10}

Percent littoral area
and protected embayments
during summer.

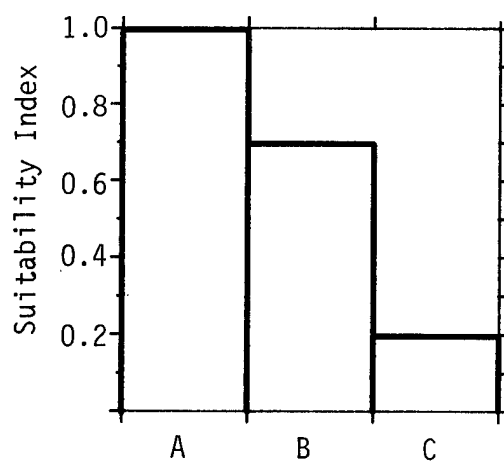


R,L

 V_{11}

Water level fluctuation before and after spawning.

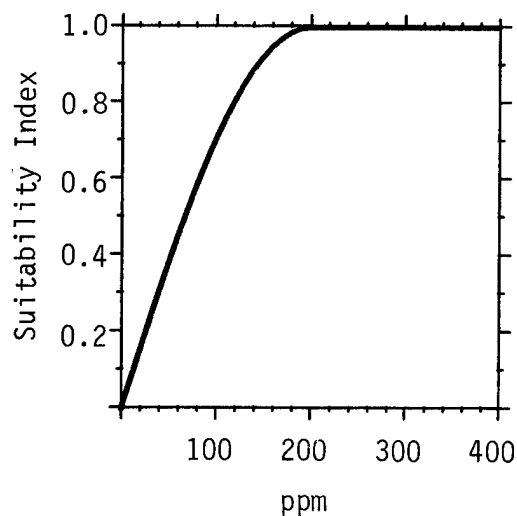
- A. Substantial rise before spawning and stable water level afterwards.
- B. Stable level before and after spawning.
- C. Stable level before spawning; decreased level after spawning.



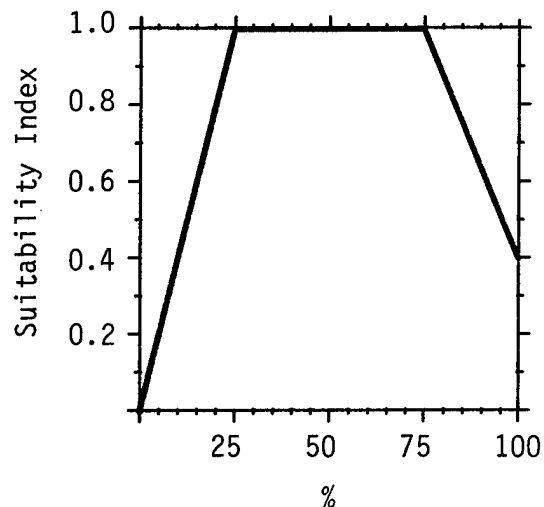
L

 V_{12}

Minimum total
dissolved solids
(TDS) during the
growing season.



R,L V_{13} Percent vegetative cover in pools, backwaters, and marsh areas (R) and in protected embayments and shoreline areas (L).



Riverine habitat suitability index equations. These equations utilize the life requisite approach and consist of four components: food-cover; water quality; reproduction; and other.

Food-Cover (C_{F-C}).

$$C_{F-C} = (V_1 \times V_{13})^{1/2}$$

Water Quality (C_{WQ}).

$$C_{WQ} = (V_2 \times V_3 \times V_4^2 \times V_6)^{1/5}$$

Note: If V_8 is added,

$$C_{WQ} = (V_2 \times V_3 \times V_4^2 \times V_6 \times V_8)^{1/6}$$

Reproduction (C_R).

$$C_R = (V_5^2 \times V_6 \times V_9^2 \times V_{11})^{1/6}, \text{ or}$$

If V_5 or $V_9 \leq 0.4$, C_R equals the lowest of the following values:
 V_5 ; V_9 ; or the above equation.

Other (C_{OT}).

$$C_{OT} = V_7$$

HSI determination.

$$HSI = (C_{F-C} \times C_{WQ} \times C_R^2 \times C_{OT})^{1/5}, \text{ or}$$

If $C_R \leq 0.4$, the HSI equals the lowest of the following values:
 C_R or the above equation.

Lacustrine habitat suitability index equations. This model utilizes the life requisite approach and consists of three components: food-cover; water quality; and reproduction.

Food-Cover (C_{F-C}).

$$C_{F-C} = (V_{10} \times V_{12}^2)^{1/3}$$

Water Quality (C_{WQ}).

Same as equation in the riverine model for water quality.

Reproduction (C_R).

Same as equation in the riverine model for reproduction.

HSI determination.

$$HSI = (C_{F-C} \times C_{WQ} \times C_R^2)^{1/4}, \text{ or}$$

If C_{WQ} or $C_R \leq 0.4$, the HSI equals the lowest of the following values: C_{WQ} , C_R , or the above equation.

Sources of data and assumptions made in developing the suitability indices are presented in Table 1.

Sample data sets from which HSI's have been generated using the riverine and lacustrine HSI equations are given in Tables 2 and 3. The data are not actual field measurements, but represent combinations that could occur in a riverine or lacustrine habitat. The HSI's calculated from the data appear to be a reasonable indication of what carrying capacity trends would be in riverine and lacustrine habitats with the listed characteristics. In its present state, the highest acceptance goal the model can meet is that it is reasonable to believe that the HSI has a positive relationship to spawning success of adults and carrying capacity of fry, juvenile, and adult bigmouth buffalo.

Interpreting Model Outputs

Habitats with an HSI of 0 may contain some bigmouth buffalo; habitats with a high HSI may contain few. The bigmouth buffalo HSI determined by use of these models will not necessarily represent the population of bigmouth buffalo in the study area. This is because the standing crop does not totally depend on the ability of an area to meet all life requisite requirements of the species. If the model is a good representation of bigmouth buffalo riverine or lacustrine habitat, the model should be positively correlated with long term average population levels in areas where bigmouth buffalo population levels are due primarily to habitat-related factors. However, this has not been tested. The proper interpretation of the HSI is one of comparison. If two habitats have different HSI's, the one with the higher HSI should have the potential to support more bigmouth buffalo than the one with the lower HSI, given that the model assumptions have not been violated.

ADDITIONAL HABITAT MODELS

Model 1

Optimum riverine conditions consist of the following, assuming that water quality is not limiting: a large river; warm, summer water temperatures (22-32° C); abundant vegetation (> 25% of sample area); and a large percentage of shallow pools, backwaters, and marshes (30-50% of water area).

Table 1. Data sources and assumptions for bigmouth buffalo suitability indices.

Variable and source	Assumption
V ₁ Trautman 1957 Johnson 1963 Kozel and Schmulbach 1976	Because bigmouth buffalo seek quiet water pools and off-channel areas, a substantial amount of these areas must exist for the habitat to be optimum.
V ₂ Trautman 1957 Johnson 1963 Walburg and Nelson 1966	Turbidity levels where the species thrives are optimum. Higher levels are tolerated but are suboptimum.
V ₃ Doudoroff and Katz 1950 Stroud 1967 European Inland Fisheries Advisory Commission 1969	pH levels that promote good production of bigmouth buffalo are optimum.
V ₄ Gammon 1973	Temperatures that are preferred by the species are assumed to be optimum.
V ₅ Canfield 1922 Swingle 1954 Johnson 1963	Temperatures that promote normal embryo development are optimum.
V ₆ U.S. Environmental Protection Agency 1976	Dissolved oxygen levels that promote healthy freshwater fish populations are optimum.
V ₇ Kallemeyn and Novotny 1977 Zittel 1978	Current velocities where adult bigmouth buffalo are found most often during the summer are optimum. Velocities that bigmouth buffalo can withstand only for short periods are suboptimum.
V ₈ Hollander and Avault 1975 Perry 1976	Salinity levels that ensure good fecundity and embryo development are optimum. Tolerance levels in laboratory tests are considered sub-optimum.
V ₉ Moen 1954 Johnson 1963 Benson 1973, 1980 Willis and Owen 1978	The type of substrate used for spawning that results in a strong year class is optimum.

Table 1. (concluded).

Variable and source	Assumption
V ₁₀ Benson 1973, 1980	The percent of littoral area and embayments associated with the highest numbers of bigmouth buffalo is optimum. Too great of a reduction of littoral area will reduce populations.
V ₁₁ Benson 1973	Water fluctuations that produce a strong year class are optimum. Fluctuations that reduce reproductive success are suboptimum to unsuitable.
V ₁₂ Walburg and Nelson 1966 Jenkins 1976	TDS levels that promote good growth or are associated with high standing crops of bigmouth buffalo are optimum.
V ₁₃ Benson 1980	The amount of vegetation present in reservoirs with high numbers of bigmouth buffalo is optimum.

Table 2. Sample data sets using the riverine HSI model.

Variable		Data set 1		Data set 2		Data set 3	
		Data	SI	Data	SI	Data	SI
Pools, backwater, and marshes (%)	V ₁	50	1.0	25	0.4	100	0.0
Turbidity (JTU)	V ₂	100	0.9	150	0.6	200	0.2
pH	V ₃	7	1.0	9	0.5	9	0.5
Temperature-adult (°C)	V ₄	27	0.9	24	0.7	36	0.6
Temperature-embryo (°C)	V ₅	15	1.0	22	0.7	25	0.5
Dissolved oxygen (ppm)	V ₆	5	1.0	5	1.0	3	0.5
Current velocity (cm/sec)	V ₇	25	1.0	50	0.8	50	0.8
Spawning substrate	V ₉	A	1.0	B	0.6	C	0.3
Water level fluctua- tion (m)	V ₁₁	A	1.0	B	0.6	C	0.3
Vegetation (%)	V ₁₃	50	1.0	50	1.0	90	0.7
<u>Component SI</u>							
C _{F-C} =			1.00		0.63		0.00
C _{WQ} =			0.94		0.68		0.45
C _R =			1.00		0.69		0.39
C _{OT} =			1.00		0.80		0.80
HSI =			0.99		0.69		0.00

Table 3. Sample data sets using the lacustrine HSI model.

Variable		Data set 1		Data set 2		Data set 3	
		Data	SI	Data	SI	Data	SI
Turbidity (JTU)	V ₂	100	0.9	150	0.6	200	0.2
pH	V ₃	7	1.0	9	0.5	9	0.5
Temperature-adult (°C)	V ₄	27	0.9	24	0.7	36	0.6
Temperature-embryo (°C)	V ₅	15	1.0	22	0.7	25	0.5
Dissolved oxygen (ppm)	V ₆	5	1.0	5	1.0	3	0.5
Spawning substrate	V ₉	A	1.0	B	0.6	B	0.6
Littoral area (%)	V ₁₀	50	1.0	10	0.4	10	0.4
Water level fluctuation (m)	V ₁₁	A	1.0	B	0.6	C	0.3
TDS (ppm)	V ₁₂	200	1.0	80	0.6	400	1.0
Vegetation (%)	V ₁₃	50	1.0	50	1.0	90	0.7
<u>Component SI</u>							
C _{F-C} =			1.00		0.63		0.67
C _{WQ} =			0.94		0.68		0.45
C _R =			1.00		0.69		0.46
HSI =			0.98		0.67		0.49

$$HSI = \frac{\text{number of above criteria met}}{4}$$

If there is little or no vegetation present during spawning season, there will probably be few fish present because vegetation is an important prerequisite for spawning success.

Model 2

Optimum lacustrine conditions consist of the following, assuming that water quality is not limiting: large reservoirs; warm, summer water temperatures (22-32° C); vegetated littoral zones; protected embayments; and optimum TDS levels.

$$HSI = \frac{\text{number of above criteria met}}{5}$$

Model 3

Use the regression equation for predicting buffalo standing crops presented by Jenkins (1967). Convert estimates to an HSI by dividing by the highest standing crop observed in the geographical area where the model is applied.

Model 4

Many factors can affect the carrying capacity of a given habitat including the variables presently in the HSI model and others not included (predation, competition, fishing mortality, barriers to migration, ice scour, or other catastrophic events). If the model assumption that species population levels are due primarily to habitat-related factors is violated, it can be inappropriate to use a HSI value as an index of carrying capacity of an area for the species and other model approaches should be considered. One approach that could be considered is to let the HSI value correspond to the lowest SI value determined for any one of the variables in the model (Inskip 1982). This approach would avoid the use of equations.

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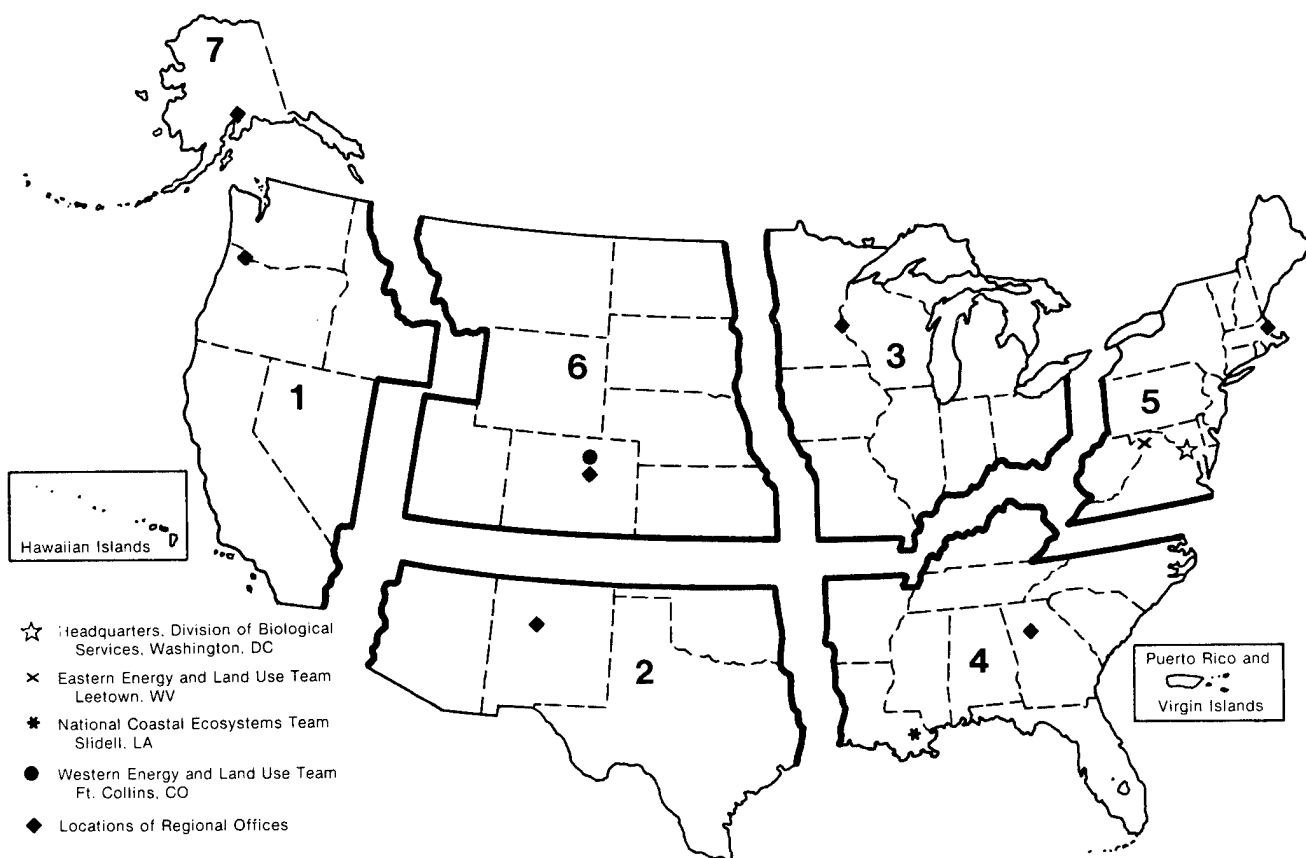
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